

RESPONDING FOR SUCROSE AND WHEEL-RUNNING REINFORCEMENT: EFFECTS OF SUCROSE CONCENTRATION AND WHEEL-RUNNING REINFORCER DURATION

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Six male albino rats were placed in running wheels and exposed to a fixed-interval 30-s schedule of lever pressing that produced either a drop of sucrose solution or the opportunity to run for a fixed duration as reinforcers. Each reinforcer type was signaled by a different stimulus. In Experiment 1, the duration of running was held constant at 15 s while the concentration of sucrose solution was varied across values of 0, 2.5, 5, 10, and 15%. As concentration decreased, postreinforcement pause duration increased and local rates decreased in the presence of the stimulus signaling sucrose. Consequently, the difference between responding in the presence of stimuli signaling wheel-running and sucrose reinforcers diminished, and at 2.5%, response functions for the two reinforcers were similar. In Experiment 2, the concentration of sucrose solution was held constant at 15% while the duration of the opportunity to run was first varied across values of 15, 45, and 90 s then subsequently across values of 5, 10, and 15 s. As run duration increased, postreinforcement pause duration in the presence of the wheel-running stimulus increased and local rates increased then decreased. In summary, inhibitory aftereffects of previous reinforcers occurred when both sucrose concentration and run duration varied; changes in responding were attributable to changes in the excitatory value of the stimuli signaling the two reinforcers.

Key words: inhibitory aftereffect, excitatory stimulus effect, wheel running, sucrose, reinforcement, fixed interval, concentration, duration, lever press, rats

The opportunity to run as a reinforcer for lever pressing generates longer postreinforcement pauses and lower rates of responding than conventional reinforcers such as a drop of sucrose solution. Belke (2000) suggested two possible mechanisms for this effect. The first was unconditioned inhibitory effects, such as fatigue or satiation, follow the termination of a reinforcer. Since running involves greater muscular movement and exertion of energy than does licking a drop of sucrose, running may generate greater fatigue. Greater fatigue may translate into a longer pause following the termination of a running reinforcer and, perhaps, a lower rate of respond-

ing. With respect to satiation, although running does not involve the ingestion of a substance, it may be the case that a process like satiation may operate. If running produces a longer-lasting satiation than does drinking sucrose solution, then rats would pause longer after running and possibly respond at a lower rate as satiation diminishes. The second mechanism involved discriminative control over the strength of responding by stimuli signaling reinforcers. Indices of response strength such as the latency to respond or the rate of responding in the presence of stimuli signaling different reinforcer magnitudes or qualities would vary as a function of the difference in the excitatory value of the stimuli. That is, in the presence of a stimulus signaling a larger reinforcer a rat may respond sooner and at a higher rate than in the presence of a stimulus signaling a smaller reinforcer.

To assess the relative roles of inhibitory aftereffects and excitatory stimulus effects between these two reinforcers, Belke (2000) used a procedure similar to that developed by Perone and Courtney (1992). Rats were exposed to a fixed interval (FI) 30-s schedule that produced 0.1 ml of 15% sucrose solution or the opportunity to run for 15 s as reinforcing consequences for lever pressing. Each

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reinforcer type was signaled by a different stimulus. Each session terminated when 100 reinforcers had been obtained and the sequence of reinforcers within a session was randomly determined. Over many sessions, a pattern of responding typical of that generated by FI schedules developed for each reinforcer type; however, responding in the presence of the stimulus signaling sucrose reinforcement typically began sooner and accelerated faster.

Postreinforcement pauses (PRPs) and local rates were assessed as a function of type of transition between successive reinforcers. Transitions were defined by type of previous and upcoming reinforcer: wheel-wheel (W-W), wheel-sucrose (W-S), sucrose-wheel (S-W), and sucrose-sucrose (S-S). The type of upcoming reinforcer determined PRP duration and local lever-pressing rates. No effect of previous reinforcer was observed. Belke (2000) concluded that differences in responding maintained by sucrose and wheel-running reinforcement were a function of differences in excitatory stimulus effects rather than inhibitory aftereffects. Belke also suggested that this difference in excitatory value may account for the difference in response rate asymptotes generated by these reinforcer values (Belke, 1998).

As Belke (2000) stated, these "results speak to the relative roles of excitatory stimulus effects and inhibitory after-effects associated with the pair of reinforcer values that generated differences in response rate asymptotes. They do not inform us about the relative roles of these effects across differing combinations of sucrose concentrations, wheel-running reinforcer durations, and reinforcement schedules" (p. 343). Thus, the present study investigated the relative roles of inhibitory aftereffects and excitatory stimulus effects for these two reinforcers over a greater range of reinforcer values. The first experiment examined the effect of manipulating sucrose concentration while wheel-running reinforcer duration remained constant and the second examined the effect of varying wheel-running reinforcer duration with sucrose concentration held constant.

GENERAL METHOD

Subjects

Six male Wistar rats obtained from Charles River Breeding Laboratories, Quebec, served

as subjects. All rats were approximately 7 months old at the start of the experiment. The rats were individually housed in polycarbonate cages (480 mm by 270 mm by 220 mm) in a holding room on a 12 hr light/dark cycle (lights on at 8:00 a.m.). Immediately after each experimental session, each rat was given an amount of food sufficient to maintain its weight at approximately 85% of a free-feeding body weight determined when each rat had reached an adult weight of approximately 400 g. Target weights varied between 330 and 340 g. Distilled water was freely available in the home cage.

Apparatus

Sessions occurred in two activity wheels (Lafayette Instruments #86041A) with diameters of 350 mm. Each wheel was located in a sound-attenuating shell with a fan for ventilation and to mask extraneous noise. Wheel revolutions were recorded by a microswitch attached to the wheel frame. Lights (24-VDC) mounted on the sides of the wheel frame illuminated the interior of the wheel chamber. A solenoid-operated brake was attached to the base of the wheel frame. When the solenoid was operated, a rubber tip attached to a metal shaft contacted the wheel and caused the wheel to stop.

A Plexiglas panel (160 mm by 165 mm by 4 mm) with a lever, two stimulus lights, and a liquid receptacle, was mounted at the opening of each wheel (70 mm by 90 mm). The lever was located 100 mm from the base of each panel. The lever was 33 mm wide and extended 20 mm from the face of the panel into the wheel chamber. The force required to activate the lever microswitch in each wheel was approximately 30 g. Located 12.5 mm above the lever were red and white 28-VDC stimulus lights (Dialco 507-3917). The diameter of each light was 7 mm and the center to center distance between the two lights was 14 mm. In one wheel, the lights were arranged so that the white light was to the left of the red. In the other, this arrangement was reversed. Adjacent to each lever was a liquid receptacle. The area of each receptacle into which sucrose solution was dispensed was 55 mm by 60 mm by 32 mm. The base of each receptacle was located 57 mm from the base of each panel. Behind the top of each receptacle was a metal clamp into which a clear

plastic cylinder (105-mm long, 38-mm diameter) and a 24-VDC General Valve Co. solenoid could be placed. A Lafayette Instruments Co. Model 80201 liquid dispenser operated the solenoid valve. Each Plexiglas panel was attached to the wheel frame by Velcro[®] strips. Control of experimental events and recording of data was handled by a Borland Turbo Pascal 4.0 program run on an IBM[®] PC computer interfaced to the wheel through the parallel port.

Procedure

Initially, 17 rats were given the opportunity to run for 30 min in running wheels used to train rats to lever press for wheel-running reinforcement. Each wheel was equipped with a retractable lever. Sessions occurred once a day for 15 days. The number of wheel revolutions was recorded for each rat on each day. After 15 days, the highest-rate runners were selected for further training. In the next phase the rats continued to receive 30-min access to the free-moving running wheel. In addition, each rat was placed in an ordinary operant conditioning chamber and lever pressing was shaped by the method of reinforcing successively closer approximations. Each lever press produced 0.1 ml of a 15% sucrose solution. When subjects reliably pressed the lever, the schedule of reinforcement was shifted from requiring only a single response per reinforcer (fixed ratio [FR] 1) to one requiring a variable number of responses averaging three (i.e., a variable-ratio [VR] schedule). This schedule remained in effect for approximately four sessions, with each session terminating when 50 sucrose reinforcers were obtained.

After four sessions on the VR 3 schedule, sessions in the operant conditioning chamber were discontinued. At this point, the retractable lever in each wheel chamber was extended during the wheel-running sessions and the opportunity to run for 60 s was contingent upon a single lever press. Retraction of the lever and movement of the wheel with the release of the brake signaled access to the running period. Each session consisted of 30 opportunities to run. The schedule of reinforcement was changed in the following sequence: FR 1, VR 3, VR 5, and VR 9. Subjects remained on each schedule for four sessions before advancing to the next schedule.

In preparation for the present study, 6 rats trained using the procedure described above were exposed to each type of reinforcement separately in the presence of different stimuli. Because Wistar rats are unlikely to discriminate differences in color, the operation of the stimulus lights signaling the two reinforcers was altered to enhance discrimination. One light was programmed to extinguish for 0.25 s (i.e., blink) when the lever was pressed and the other to remain lit (i.e., no blink) when the lever was pressed. Blinking was associated with different reinforcers in the two wheels. In one wheel, the red stimulus light that blinked when the lever was pressed signaled wheel running and in the other it signaled sucrose. Programming the stimulus to signal the reinforcer following, rather than before, a lever press raises the possibility that blinking could function as a conditioned reinforcer or that the first lever press following a reinforcer was an information-seeking response. In either case, the dependent measures, PRPs and local lever-pressing rates, might be affected. Belke (2000) addressed this issue by assessing PRPs and local lever-pressing rates in the same rats when the stimuli signalling the two reinforcers blinked or did not blink. Analysis of PRPs showed a significant effect of reinforcer type (wheel running, sucrose), but no effect of stimulus condition (blink, no blink) and no interaction of stimulus condition with reinforcer type. Analysis of local rates produced the same results.

During this training phase, the rats were placed in the running wheels with the Plexiglas panels, as described in the Apparatus section, and exposed to tandem FR 1 variable-interval (VI) 30-s schedules. Each session terminated when 50 reinforcers had been obtained. Only a single type of reinforcer, either the opportunity to run for 15 s or 0.1 ml of 15% sucrose solution, was scheduled and signaled during these sessions. The rats were exposed to alternating blocks of five sessions of responding for wheel-running and sucrose reinforcers. These conditions remained in effect for 80 sessions.

Following this training phase, the rats were exposed to a standard fixed-interval (FI) 30-s schedule of reinforcement with either the opportunity to run for 15 s or 0.1 ml of a 15% sucrose solution as the reinforcing conse-

quence. The type of reinforcement that occurred when the schedule requirement was met was determined by random selection from a set of two values. When the reinforcement requirement was met, the stimulus light signaling a wheel-running reinforcer was extinguished for the duration of the reinforcement period whereas the stimulus signaling sucrose reinforcement was extinguished for 0.5 s. Each session terminated when 100 reinforcements were obtained.

Lever presses, time spent lever pressing, PRPs, and wheel revolutions (for wheel-running reinforcement only) were recorded for each reinforcer and cumulatively for the entire session. Wheel-running rate was calculated as the total number of revolutions divided by the total time during which running could occur and expressed as revolutions per minute. An overall lever-pressing rate was calculated as total lever presses that occurred while the reinforcement schedule was in effect divided by time during which the schedule was in effect. This rate was expressed as lever presses per minute. A local lever-pressing rate was calculated as total lever presses that occurred from the press that terminated the PRP to the press that produced the reinforcement divided by time during which these presses occurred, and expressed as lever presses per minute. A postreinforcement pause was measured as the interval between the termination of a reinforcer and the first lever press in the presence of a stimulus signaling a reinforcer. In addition, lever presses during successive 5-s segments of the 30-s schedule interval were cumulated over the entire session separately for intervals that terminated in wheel-running and sucrose reinforcement. Finally, wheel revolutions during successive 5-s segments of the 15-s reinforcement period were cumulated across all wheel-running reinforcers within a session.

EXPERIMENT 1

Experiment 1 assessed the effects of varying sucrose concentration on responding maintained by sucrose and wheel-running reinforcement. The specific purpose was to assess changes in responding in terms of unconditioned inhibitory aftereffects following each reinforcer type and the excitatory stim-

Table 1

The order of sucrose concentrations for each rat.

Rat	Percent sucrose concentration (w/v)				
	0	2.5	5	10	15
IB6	5	1	2	3	4
IB7	5	4	3	2	1
IB10	5	3	1	2	4
IB12	5	3	1	4	2
IB14	5	4	2	3	1
IB15	5	2	4	1	3

ulus value of stimuli signaling the two reinforcers.

METHOD

Procedure

Each rat was exposed to a different order of sucrose concentrations. Table 1 presents the order of sucrose concentrations for each rat. Each concentration was in effect for 25 sessions. Rats IB6, IB15, and IB10 were assigned to the wheel where wheel-running reinforcement was associated with a nonblinking white stimulus light, and the remaining rats, IB7, IB12, and IB14, were assigned to the wheel where wheel-running reinforcement was associated with a blinking red stimulus light. Immediately following the completion of these conditions, all rats were exposed to five sessions where the concentration of sucrose was reduced to 0% (i.e., water). The number of sessions was limited to five because of the tendency for session time to increase markedly and to limit the extent of extinction of the association between sucrose reinforcement and the stimulus light.

RESULTS

Figure 1 shows mean response rates (presses per minute) in successive 5-s segments of the FI 30-s interval for the group. The upper panel depicts response rates in the presence of the sucrose stimulus across the different concentrations. The lower panel depicts rates in the presence of the wheel-running stimulus. Response rates were obtained from the final five sessions for each of the concentrations. Response rate functions in the presence of both stimuli showed a pattern of responding consistent with an FI schedule. Responding was lowest early in the interval and increased as the interval elapsed toward

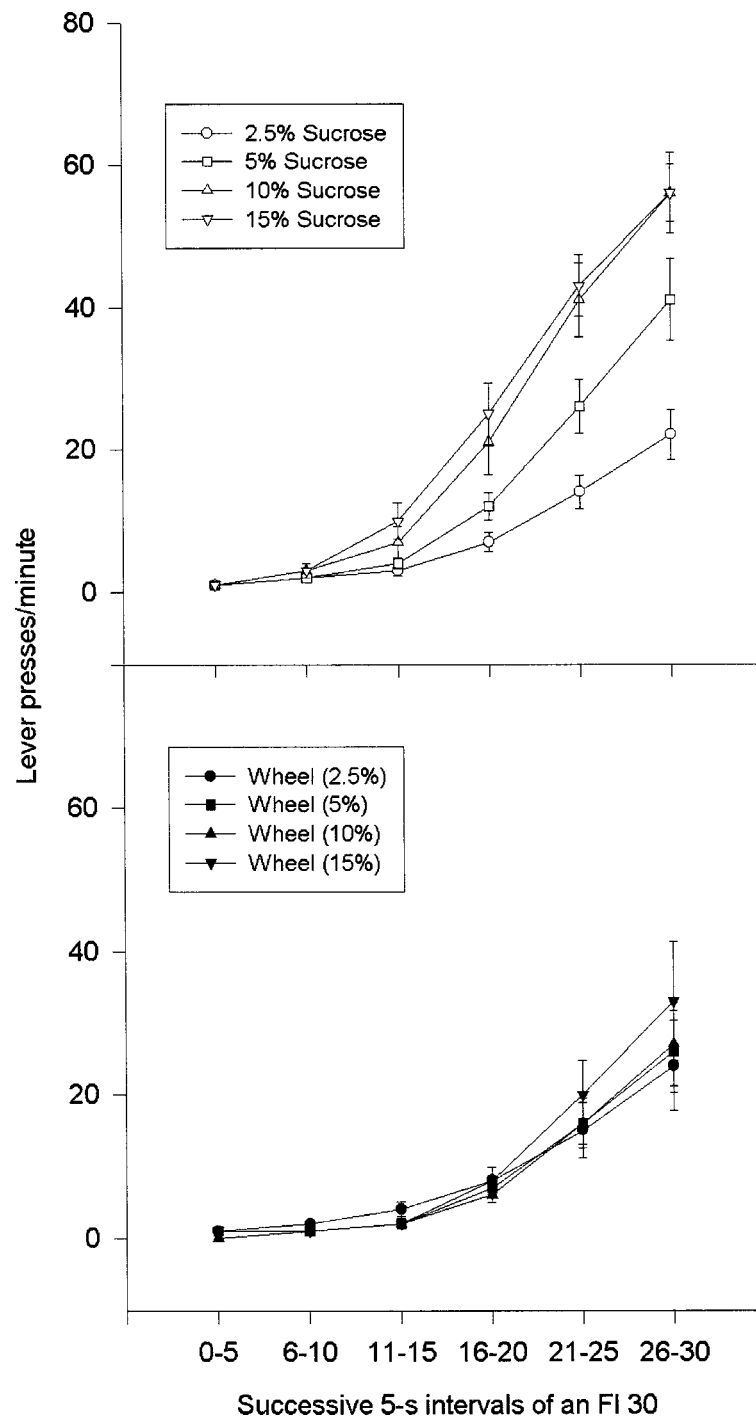


Fig. 1. Mean response rates (lever presses per minute) in successive 5-s segments of an FI 30-s reinforcement interval in the presence of stimuli signaling sucrose (top) and wheel running (bottom) for the 2.5, 5, 10 and 15% sucrose concentration conditions for the group. Standard errors are shown for each data point.

reinforcement. Response rate functions varied with concentration in the presence of a sucrose stimulus, but not in the presence of a stimulus signaling an opportunity to run. A series of one way repeated measures analyses of variance (ANOVAs) assessing the effect of concentration on response rates at each 5-s interval in the presence of the sucrose stimulus showed significant effects (with alpha set at .0083) for all intervals beyond 10 s. An equivalent analysis for responding in the presence of the wheel-running stimulus yielded no significant effects for any interval.

Figure 2 shows the response rate functions depicted in Figure 1 arranged by concentration rather than signaled reinforcer. Data from the 0% concentration are included to demonstrate that the function generated by 2.5% fell on a scale of value between 0 and 15%. At the highest concentration, the response rate function for sucrose was higher than that for wheel running. As concentration decreased from 15 to 2.5%, the difference between the two response rate functions decreased and then disappeared. At 0%, the difference reversed with the function for wheel running higher than that for sucrose and the sucrose function relatively flat and close to zero. Arranged in this manner, these data suggest that responding generated by a 15-s opportunity to run was similar to that generated by a drop of 2.5% sucrose solution.

Figure 3 shows overall response rates as a function of sucrose concentration in the presence of the stimuli signaling sucrose and wheel running for each rat and the group. This figure illustrates the differential effect of sucrose concentration in the presence of the stimuli signaling different reinforcer types. A repeated measures ANOVA with reinforcer type (sucrose, wheel) and concentration (2.5, 5, 10, 15%) as within subject variables yielded significant main effects of reinforcer type, $F_{(1,5)} = 8.18, p < .05$; and concentration, $F_{(3,15)} = 41.71, p < .05$; as well as a significant interaction, $F_{(3,15)} = 45.72, p < .05$. Of greatest interest is the interaction. The effect of concentration on overall response rates depended on reinforcer type. At the lowest concentration, overall response rates did not differ by reinforcer type. As concentration increased, response rates in the presence of the sucrose stimulus increased, while rates in

the presence of the wheel-running stimulus were relatively unaffected.

Figure 4 shows median PRP durations as a function of combinations of previous and upcoming reinforcer types and sucrose concentration for each rat and the group. Median PRPs were obtained from the distribution of PRPs from the last five sessions in each condition. Median rather than mean values were used due to the sensitivity of means to large values. In the presence of a sucrose stimulus, median PRP duration decreased as concentration increased.

In the presence of a wheel-running stimulus, median PRP duration did not vary with concentration. A 3-way repeated-measures ANOVA with concentration (2.5, 5, 10, 15), previous reinforcer type (wheel, sucrose) and upcoming reinforcer type (wheel, sucrose) as within-subject variables revealed significant main effects of concentration [$F_{(3,15)} = 8.04, p < .05$] and upcoming reinforcer type [$F_{(1,5)} = 7.69, p < .05$], but no main effect of previous reinforcer [$F_{(1,5)} = 1.58, ns$]. Significant interactions between concentration and upcoming reinforcer type [$F_{(3,15)} = 17.85, p < .05$] and concentration and previous reinforcer type. [$F_{(3,15)} = 4.03, p < .05$] also occurred. With respect to the interaction with upcoming reinforcer type, as concentration increased, median PRPs decreased in the presence of the sucrose stimulus, but not in the presence of the wheel-running stimulus. Mean median PRPs for the 2.5, 5, 10, and 15% concentrations were 21.55, 20.44, 17.03, and 15.07 s when the next reinforcer was sucrose and 23.47, 24.16, 24.12, and 23.30 s when the next reinforcer was wheel running.

With respect to the interaction with previous reinforcer type, at the lowest concentration, median PRPs following wheel running were longer than those following sucrose. As concentration increased, median PRPs following wheel running decreased systematically while those following sucrose remained relatively unaffected. Mean median PRPs for the 2.5, 5, 10, and 15% concentrations were 23.92, 23.42, 21.02, and 18.66 s when the previous reinforcer was wheel running and 21.10, 21.17, 20.12, and 19.71 s when the previous reinforcer was sucrose.

Figure 5 shows local lever-pressing rates as a function of combinations of previous and upcoming reinforcer types and sucrose con-

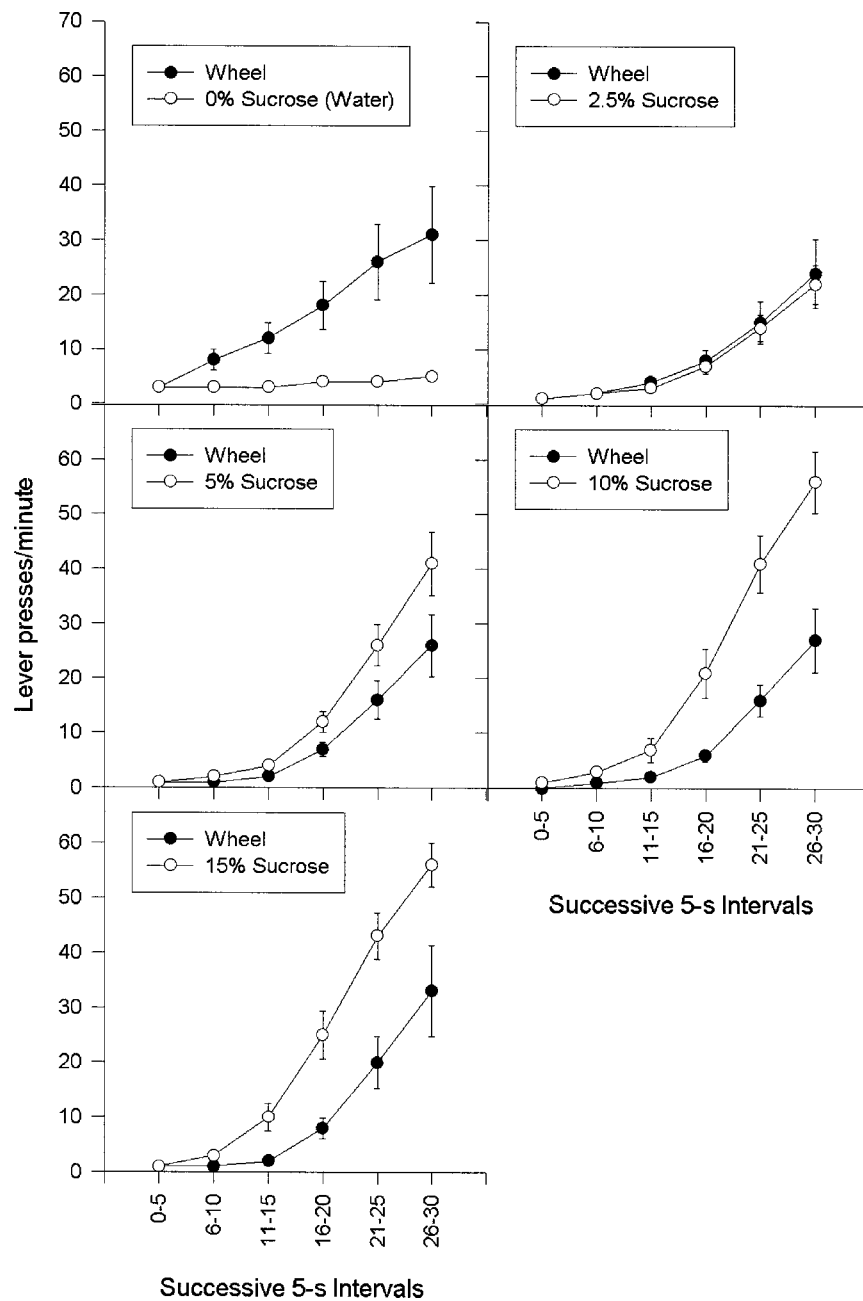


Fig. 2. Mean response rates (lever presses per minute) in successive 5-s segments of an FI 30-s reinforcement interval in the presence of stimuli signaling sucrose and wheel-running reinforcers at each sucrose concentration. Data from the 0% sucrose concentration are included. Standard errors are shown for each data point.

centration for each rat and the group. Variation in local response rates was less systematic. A three-way repeated measures ANOVA equivalent to that conducted with PRPs revealed a significant main effect of concentra-

tion, $F_{(3,15)} = 18.07$, $p < .05$, and a significant concentration by upcoming reinforcer interaction, $F_{(3,15)} = 8.04$, $p < .05$. At the lowest concentration local rates did not differ. As concentration increased, local rates in the

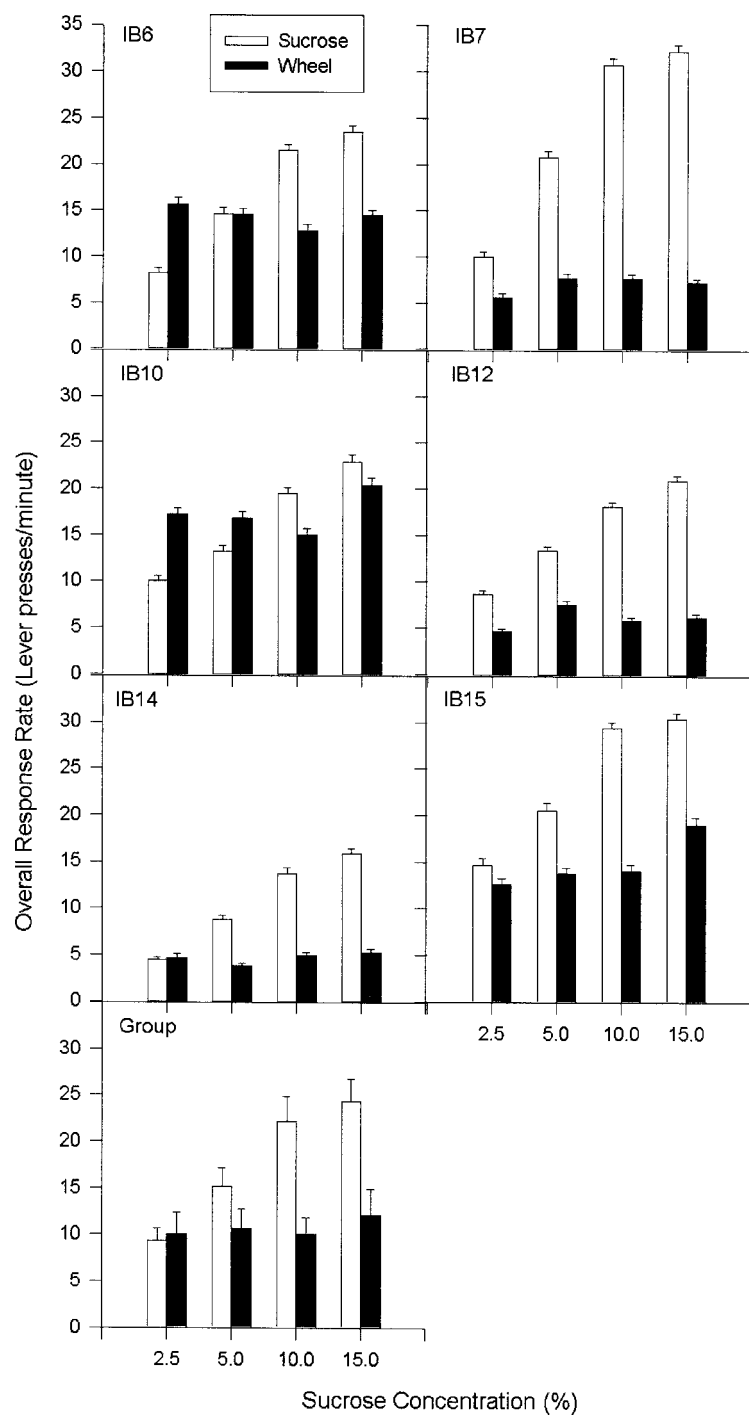


Fig. 3. Mean overall response rates (presses per minute) in the presence of sucrose and wheel-running stimuli as a function of sucrose concentration for each rat and the group. Standard errors are shown for each mean.

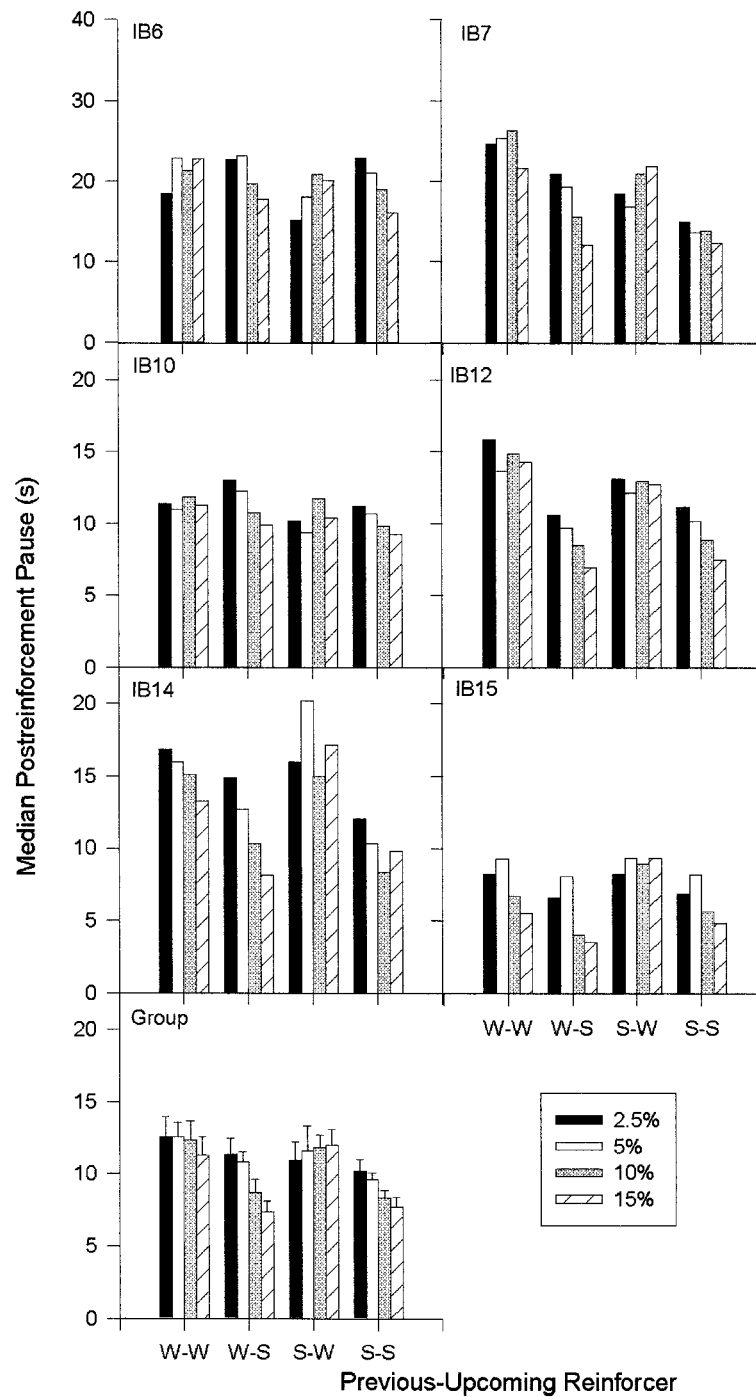


Fig. 4. Median postreinforcement pauses (s) as a function of transition type and concentration for each rat and the group. Transitions are defined by the combination of the types of previous and upcoming reinforcers. Wheel-running and sucrose reinforcers are denoted with a W and an S, respectively. Standard errors are shown for group means.

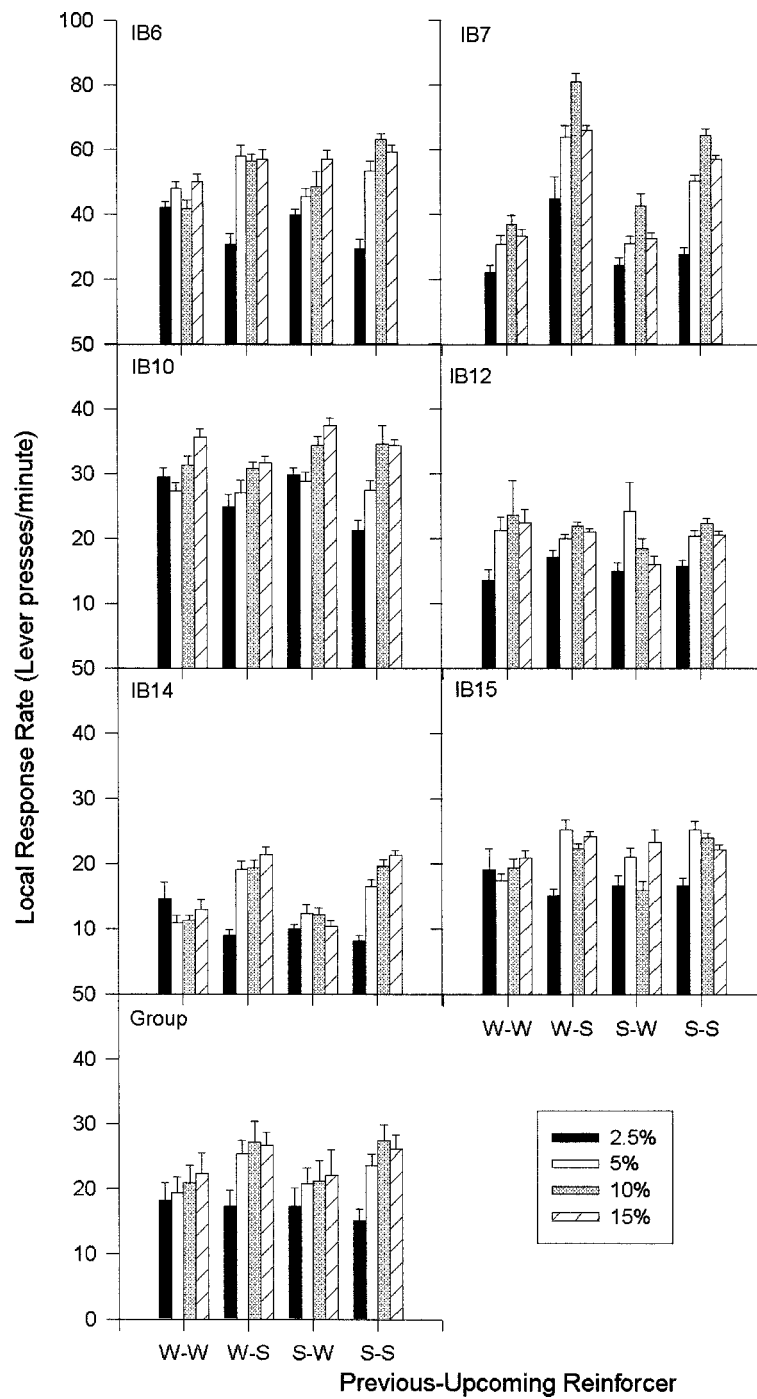


Fig. 5. Mean local lever-pressing rates (presses per minute) as a function of transition type and concentration for each rat and the group. Transitions are defined by the combination of the types of previous and upcoming reinforcers. Wheel-running and sucrose reinforcers are denoted with a W and an S, respectively. Standard errors are shown for each mean value.

presence of both stimuli increased, but to a greater degree in the presence of the sucrose stimulus. In the presence of the stimulus signaling sucrose, local rates generated by the 2.5, 5, 10 and 15% concentrations were 27.99, 47.15, 53.64, and 52.40 presses per minute. In the presence of the wheel-running stimulus, the equivalent values were 32.5, 37.22, 38.63, and 42.09 presses per minute.

Figure 6 depicts mean wheel-running rates by concentration in successive 5-s segments of the 15-s reinforcement interval for each rat and the group. In general, running was not affected by sucrose concentration. Mean wheel-running rates for the 2.5, 5, 10, and 15% concentrations were 36.58, 37.24, 36.29, and 36.39 revolutions per minute. A repeated measures ANOVA with concentration (2.5, 5, 10, 15) and 5-s interval as within-subject variables showed a significant main effect of interval, $F_{(2,10)} = 8.64$, $p < .05$, and a significant concentration by interval interaction, $F_{(6,30)} = 3.62$, $p < .05$. Within the reinforcer interval, wheel-running rates increased from the first to the second segment and then decreased in the last segment. The lower running rate in the first interval resulted from the transition between lever pressing and running. The interaction reflects a systematic decrease in running rate with concentration in the last interval that was not present in the previous two intervals.

DISCUSSION

As demonstrated by Belke (2000), rats responded differently in the presence of stimuli signaling sucrose and wheel-running reinforcers. Although responding in the presence of both stimuli showed a pattern of responding typical of that observed on FI schedules, responding in the presence of a stimulus signaling sucrose generally began sooner and accelerated more rapidly within the interval. Varying the concentration of the sucrose solution produced systematic changes in the responding in the presence of the sucrose stimulus, while responding in the presence of the wheel-running stimulus was unaffected. As the concentration of sucrose decreased, the difference in response rate functions in the presence of the two stimuli diminished and at 2.5% the functions were similar. Thus, the value of an opportunity to run for 15 s was approximately equal to the value of a drop of

2.5% sucrose solution for these rats. At concentrations greater than 2.5%, under the same durations of deprivation of running and food, the maximum amount of responding maintained by run reinforcers was less than the maximum amount maintained by sucrose. In this sense, then, run reinforcers were weaker than sucrose reinforcers, a result consistent with Collier's (1970) suggestion that "since in the long run, it is better to eat than to run, running, as we have shown, is a weak reinforcer" (p. 575).

Analyses of PRPs and local rates showed that PRPs were shorter and local rates were higher when the upcoming reinforcer was sucrose. As concentration increased, the excitatory value of the stimulus signaling sucrose increased. Rats initiated responding earlier and responded at higher rates as the excitatory value of the sucrose stimulus increased. The effect of this change in concentration was largely, but not entirely, limited to responding in the presence of the opportunity to obtain sucrose. Local rates in the presence of a wheel-running stimulus also increased with concentration, but to a lesser degree. Apparently, increased activation of responding by the sucrose stimulus generalized beyond the context of this stimulus.

There was no evidence that changes in responding in the presence of either the sucrose or the wheel-running stimulus resulted from a change in inhibitory aftereffects. As sucrose concentration decreased, a drop of sugar water would produce less momentary satiation and shorter pauses. This did not occur. Instead, pauses following sucrose did not change while pauses following running appeared to lengthen. It does not seem reasonable to suggest that decreasing sucrose concentration increased inhibitory aftereffects associated with running. Indeed, in the 0% condition, pauses following running decreased rather than increased. A possible explanation is that wheel running has greater inhibitory aftereffects than sucrose, but the expression of this difference was masked by the excitatory effects of sucrose on responding in the presence of stimuli signaling both reinforcers. This might also account for the absence of an effect of previous reinforcer in Belke's (2000) study. In that study, the opportunity to run was 15 s and the concentration of the sucrose solution was 15%.

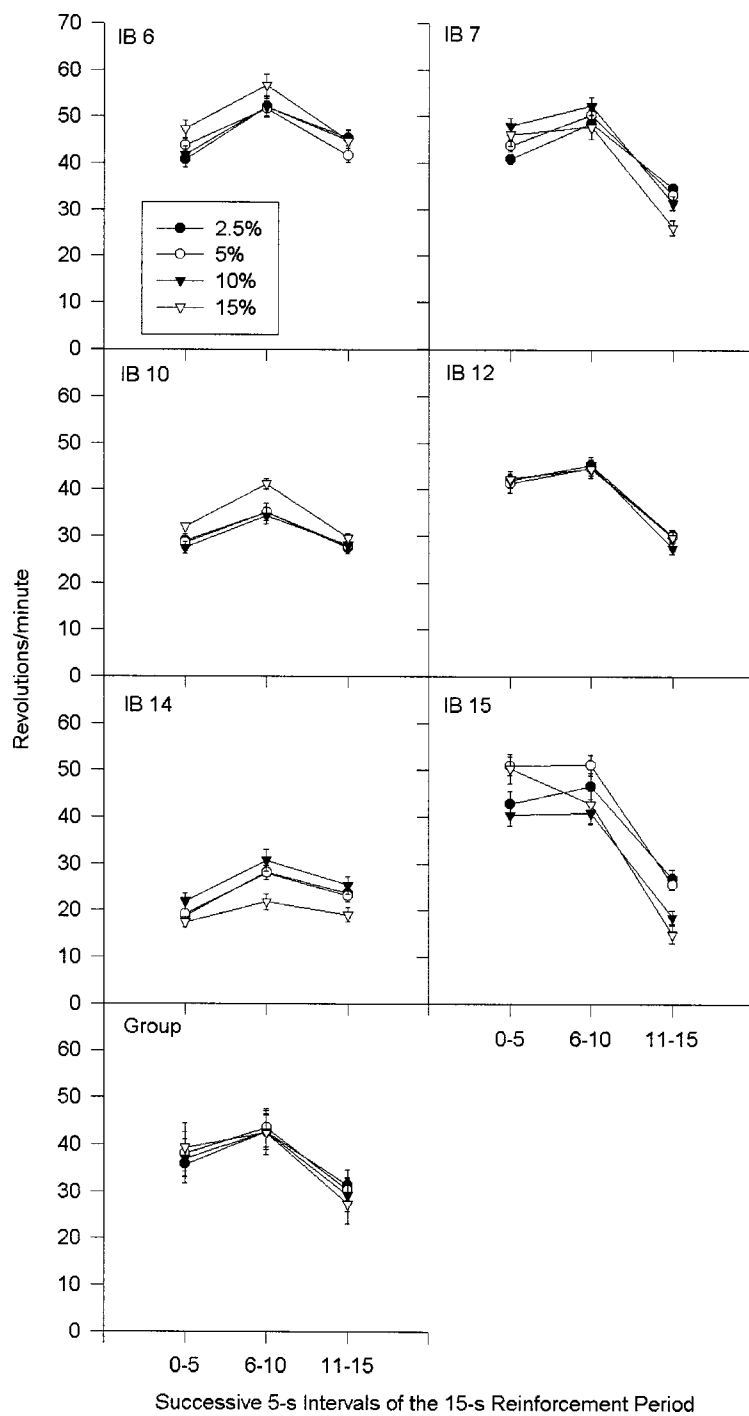


Fig. 6. Mean wheel-running rates (revolutions per minute) in successive 5-s segments of the 15-s wheel-running reinforcer as a function of sucrose concentration for each rat and the group. Standard errors are shown for each mean.

EXPERIMENT 2

Experiment 1 demonstrated that varying sucrose concentration affected responding in the presence of a stimulus signaling a sucrose reinforcer but had no effect on responding in the presence of a stimulus signaling wheel running. In Experiment 2, sucrose concentration was held constant at 15% while wheel-running reinforcer duration was varied initially over durations of 15, 45, and 90 s and then later over durations of 5, 10, and 15 s. The addition of this latter set of durations was designed to increase the range over which the effects of reinforcer duration on operant responding could be assessed. The purpose of this study was to assess changes in inhibitory aftereffects and excitatory stimulus effects associated with the two reinforcers as a function of changes in the duration of an opportunity to run.

METHOD

Procedure

The procedure was modified from that described above. In Experiment 1, the sequence of reinforcer types within a session was determined by random selection from a list of two values and the total number of reinforcers in a session was 100. Predetermined lists of values representing sequences of reinforcer types were created for this experiment. Each list contained 101 values. Within each list, the same type of reinforcer could occur no more than four times in a row and each list was designed to generate an equal number of the four different types of transitions. Six different lists were created and rats were exposed in a fixed order to a different list on each successive day. That is, after the sixth list was completed, the rats were started back on the first list. Different lists were generated for each wheel.

Initially, each rat was exposed to a different order of three reinforcer durations, 15, 45, and 90 s. Following completion of these durations, the rats were exposed to additional durations, 5 and 10 s, to extend the range and assess trends observed with the longer durations. The rats were exposed to these additional durations 140 days after completion of the original set of durations. In the interim, the rats experienced prerunning and prefeeding manipulations. Following these ma-

Table 2

The order of wheel-running reinforcer durations for each rat for the long (15, 45, 90 s) and short (5, 10, 15 s) sets of durations.

Rat	Reinforcer duration (s)					
	15	45	90	5	10	15
IB6	1	2	3	5	6	4
IB7	1	3	2	6	5	4
IB10	3	2	1	5	6	4
IB12	3	1	2	5	6	4
IB14	2	3	1	6	5	4
IB15	2	1	3	6	5	4

nipulations, the rats were returned to the 15-s duration condition for 25 days prior to exposure to the additional conditions. Table 2 presents the order of durations for each rat. Each duration was in effect for 25 sessions. Wheel assignments remained the same as described in Experiment 1.

RESULTS

Figure 7 shows mean response rates (presses per minute) in successive 5-s segments of the FI 30-s interval for the group. The upper panel depicts response rates in the presence of the sucrose stimulus for the 5, 10, 15, 15, 45, and 90-s duration conditions. The lower panel depicts response rate functions in the presence of the wheel-running stimulus. Response rates were obtained from the final five sessions at each duration. Duration of opportunity to run had no effect on responding in the presence of the sucrose stimulus. Responding in the presence of the wheel-running stimulus was also largely unaffected until the duration of the wheel-running reinforcer exceeded 15 s. Beyond 15 s, as duration increased, response rate functions systematically decreased. Figure 8, in which response rate functions are arranged by duration rather than signalled reinforcer, also illustrates the lack of an effect of duration up to 15 s. Response rate functions in the presence of the two stimuli remained unchanged for the 5, 10, 15, and 15-s durations. For the 45 and 90-s durations, responding in the presence of the wheel-running stimulus declined.

Figure 9 shows overall response rates as a function of duration in the presence of stimuli signaling sucrose and wheel running across all reinforcer durations. To assess if re-

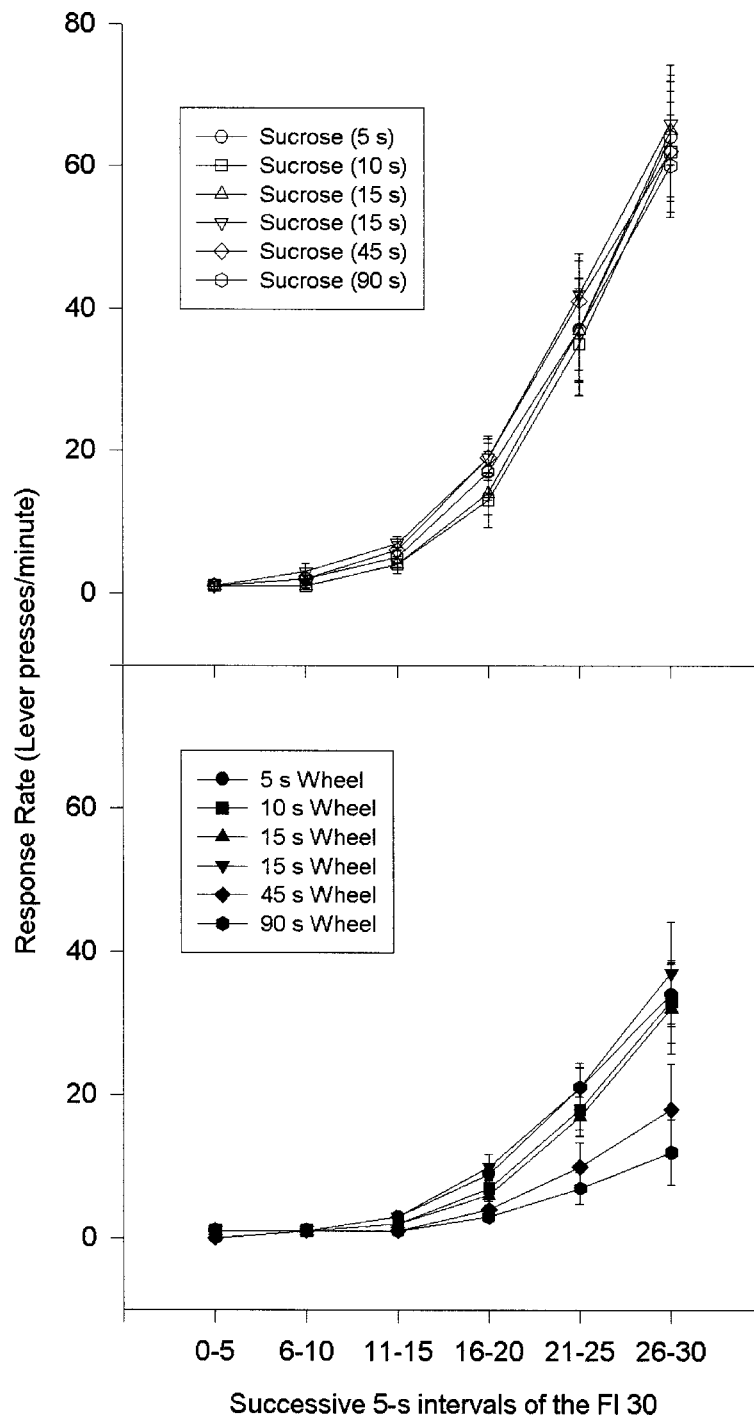


Fig. 7. Mean response rates (lever presses per minute) in successive 5-s segments of an FI 30-s reinforcement interval in the presence of stimuli signaling sucrose (top) and wheel running (bottom) for the 5, 10, 15, 15, 45, and 90-s reinforcer duration conditions for the group. Standard errors are shown for each data point.

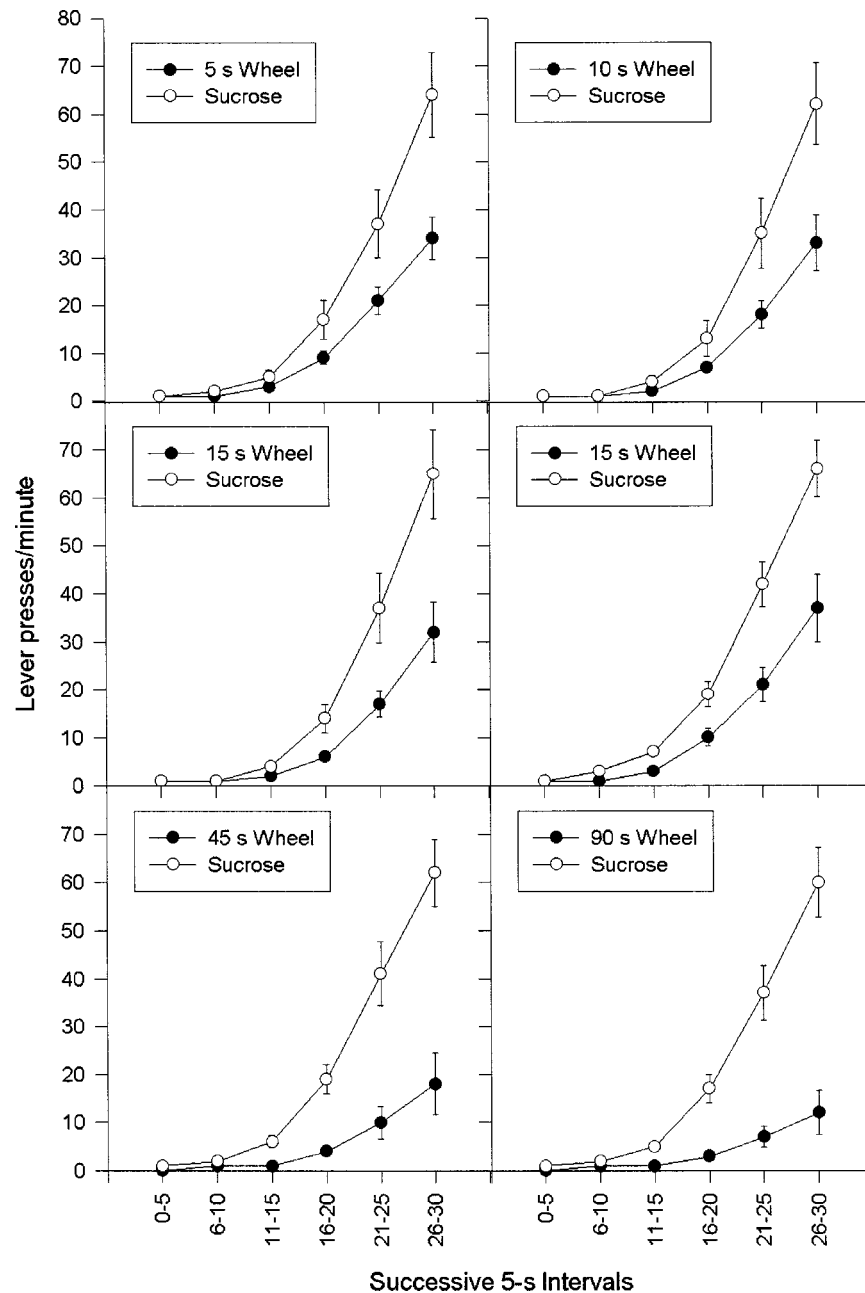


Fig. 8. Mean response rates (lever presses per minute) in successive 5-s segments of an FI 30-s reinforcement interval in the presence of stimuli signaling sucrose and wheel-running reinforcers at each wheel-running reinforcer duration. Standard errors are shown for each data point.

sponding differed between the first and second exposures to the 15-s durations, a repeated measures ANOVA was conducted with reinforcer type (wheel, sucrose) and exposure (first, second) as within-subject variables. This analysis revealed a significant effect of

reinforcer type, $F_{(1,5)} = 26.41$, $p < .05$, but no effect of exposure, $F_{(1,5)} = 2.43$, ns , and no interaction, $F_{(1,5)} = 0.02$, ns . Based on this analysis, data from both series were combined with each 15-s duration condition still represented in the analysis.

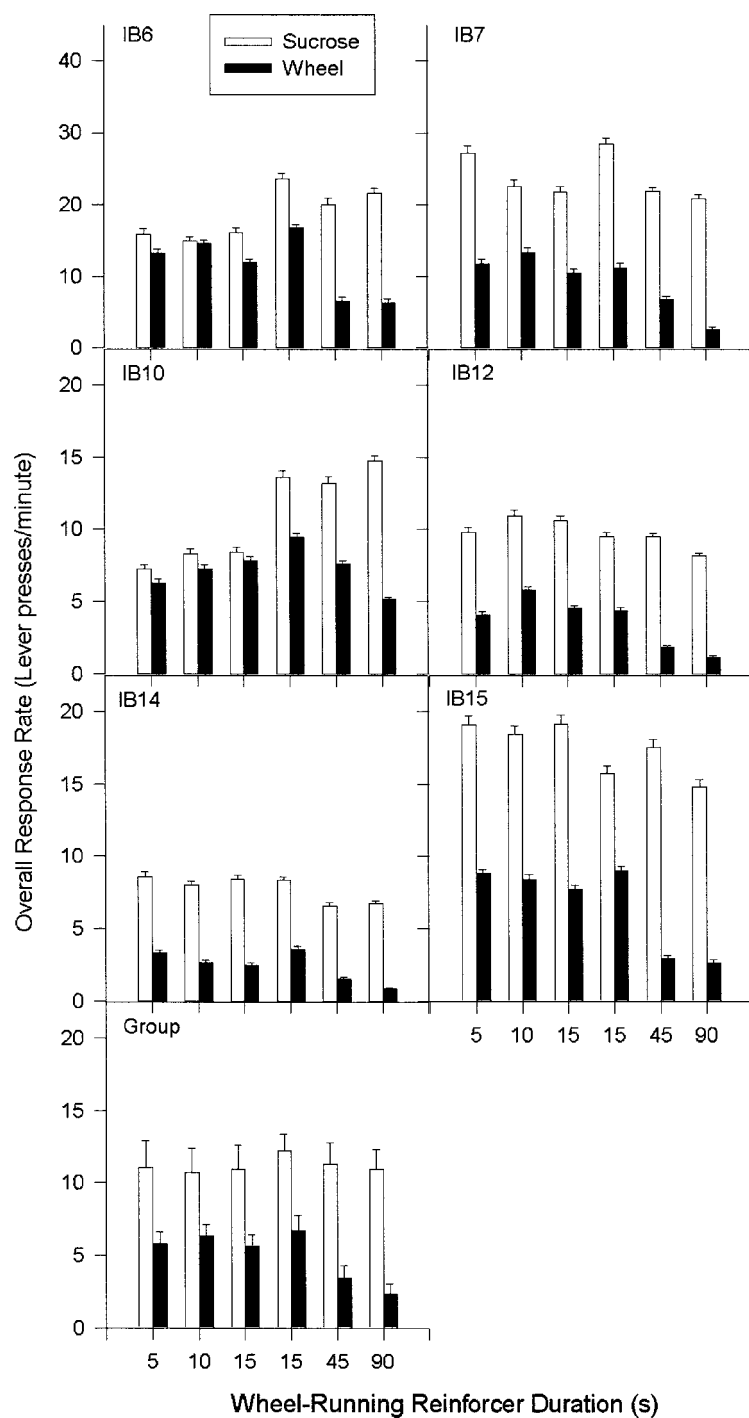


Fig. 9. Mean overall response rates (presses per minute) in the presence of sucrose and wheel-running stimuli as a function of run duration for each rat and the group. Standard errors are shown for each mean.

Overall response rates were higher in the presence of a sucrose stimulus, and duration of opportunity to run had little effect on responding in the presence of this stimulus. In the presence of a wheel-running stimulus, overall response rates did not vary between 5 and 15 s, then decreased systematically with duration. A repeated measures ANOVA with reinforcer type (wheel, sucrose) and duration (5, 10, 15, 15, 45, 90 s) as within-subject variables yielded significant main effects of reinforcer type, $F_{(1,5)} = 30.57$, $p < .05$, and duration, $F_{(5,25)} = 3.35$, $p < .05$, as well as a significant interaction, $F_{(5,25)} = 5.19$, $p < .05$. Mean overall response rates in the presence of sucrose and wheel-running stimuli were 22.38 and 10.11 presses per minute, respectively. In terms of the interaction, separate repeated measures ANOVAs confirmed that response rates varied with duration in the presence of the stimulus signaling wheel-running reinforcement, $F_{(5,25)} = 16.71$, $p < .025$, but not the stimulus signaling sucrose reinforcement, $F_{(5,25)} = 0.45$, *ns*. Limiting the analysis to the 5, 10, 15, and 15-s conditions, a repeated measures ANOVA with reinforcer type and duration as within-subject variables showed that although the main effect of reinforcer type remained, $F_{(1,5)} = 16.99$, $p < .05$, there was no effect of duration, $F_{(3,15)} = 1.36$, *ns*, and no interaction, $F_{(3,15)} = 0.61$, *ns*.

Figure 10 shows median postreinforcement pause durations broken down by transition and reinforcer duration. Unlike overall response rates, median PRPs differed between exposures to the 15-s conditions. A paired *t*-test comparison of medians collapsed across transitions showed that, on average, median PRPs were systematically longer during the second exposure, $t(5) = 5.25$, $p < .05$. Average median PRPs for the first and second exposures were 18.59 and 20.86 s. For this reason, separate analyses were conducted for each set of reinforcer durations.

For the 5, 10, and 15-s conditions, a repeated measures ANOVA with duration, upcoming reinforcer, and previous reinforcer as within-subject variables revealed a significant effect of duration, $F_{(2,10)} = 8.66$, $p < .05$, but no effect of previous or upcoming reinforcer. On average, mean median PRPs were shorter for the 5 (18.86 s), than for the 10 (20.78 s), or 15-s (20.86 s) conditions.

For the 15, 45, and 90-s conditions, an equivalent analysis produced significant main effects of duration, $F_{(2,10)} = 10.93$, $p < .05$, and upcoming reinforcer, $F_{(1,5)} = 18.15$, $p < .05$, as well as significant interactions between duration and upcoming reinforcer, $F_{(2,10)} = 9.92$, $p < .05$, and between previous and upcoming reinforcer, $F_{(1,5)} = 6.43$, $p = .05$. PRPs did not vary with duration when the next reinforcer was sucrose, but did when it was the opportunity to run. Mean median pauses in the presence of a sucrose stimulus for the 15, 45, and 90-s conditions were 16.17, 16.85, and 16.38 s, respectively. Equivalent values in the presence of a wheel stimulus were 21.01, 31.55, and 44.17 s.

When the next reinforcer was sucrose, mean median PRPs did not differ with prior reinforcer type (sucrose, 16.67 s; wheel, 16.26 s). When the next reinforcer was wheel running, however, mean median PRPs were longer when the previous reinforcer was wheel running (35.40 s) than when it was sucrose (29.09 s). Although this interaction provides evidence of an aftereffect, the aftereffect did not vary with wheel-running duration. Mean differences between W-W and S-W transitions for the 15, 45, and 90-s duration conditions were 3.36, 7.63, and 7.91 s, respectively. A repeated measures ANOVA showed no effect of duration, $F_{(2,10)} = 0.76$, *ns*.

Figure 11 depicts local lever-pressing rates broken down by transition and reinforcer duration. Local lever-pressing rates, unlike median PRPs, did not differ between 15-s conditions, ($t(5) = 0.27$, *ns*). Mean local response rates for the first and second exposures were 52.57 and 51.31 presses per minute. Although local rates did not differ between 15-s condition, data from the different sets of durations were analyzed separately to parallel the analysis of median PRPs.

For the 5, 10, and 15-s durations, a repeated measures ANOVA revealed significant main effects of duration, $F_{(2,10)} = 4.13$, $p = .05$, and upcoming reinforcer, $F_{(1,5)} = 10.04$, $p < .05$. Mean local rates were lower for the 5 (49.13 presses per minute) than the 10 (52.74 presses per minute) and 15-s (52.57 presses per minute) durations and higher when the upcoming reinforcer was sucrose (60.81 presses per minute) than running (42.15 presses per minute). For the 15, 45, and 90-s durations, the same analysis pro-

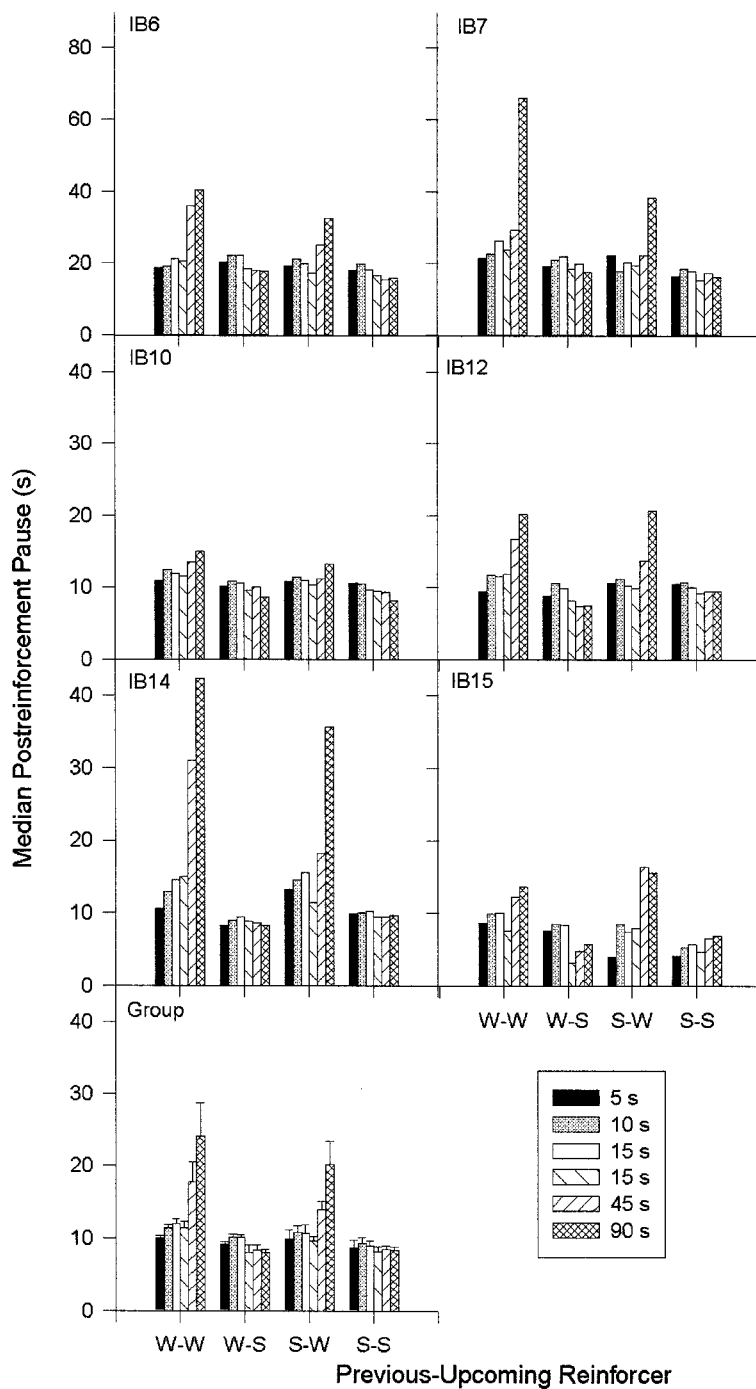


Fig. 10. Median postreinforcement pauses (s) as a function of transition type and wheel-running reinforcer duration for the 5, 10, 15, 15, 45, and 90-s wheel-running reinforcer durations for each rat and the group. Transitions are defined by the combination of the types of previous and upcoming reinforcers. Wheel-running and sucrose reinforcers are denoted with a W and an S, respectively. Standard errors are shown for group means.

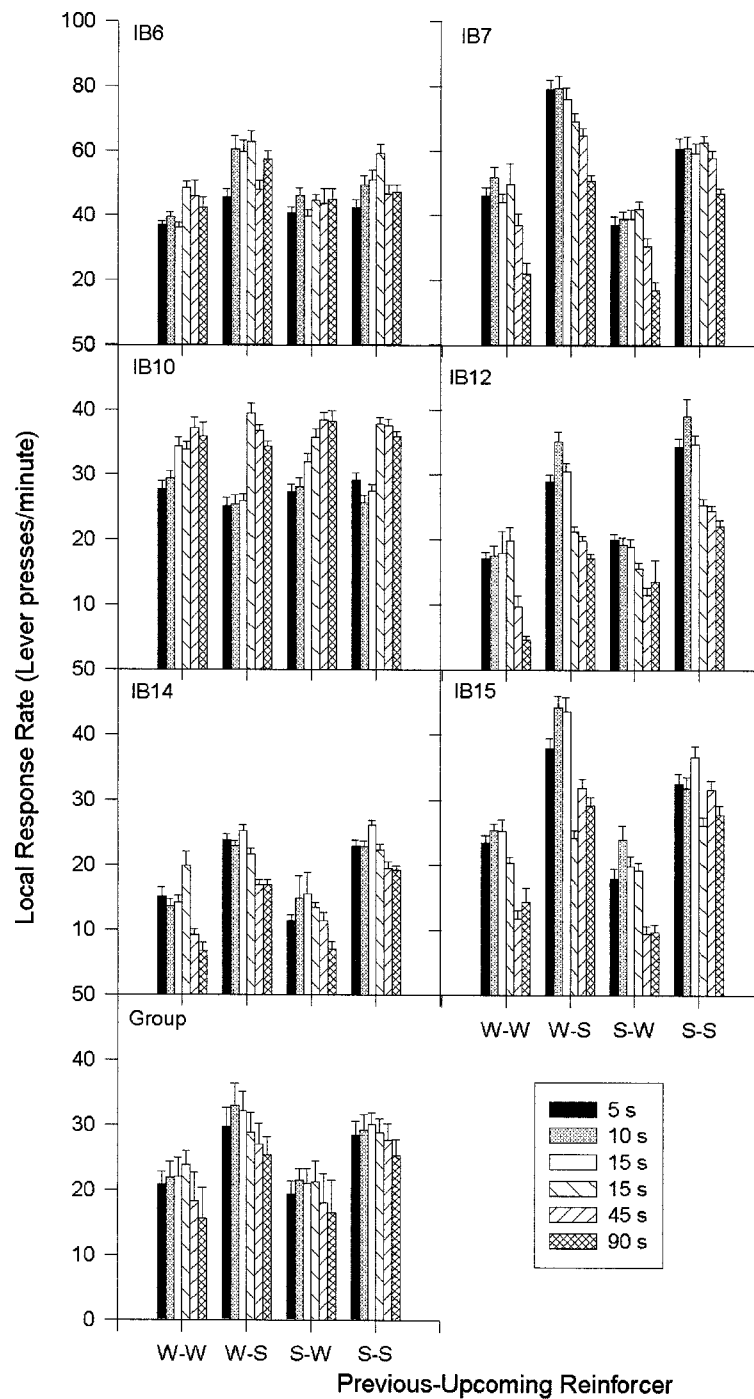


Fig. 11. Mean local lever-pressing rates (presses per minute) as a function of transition type and wheel-running reinforcer duration for the 5, 10, 15, 15, 45, and 90-s wheel-running reinforcer durations for each rat and the group. Transitions are defined by the combination of the types of previous and upcoming reinforcers. Wheel-running and sucrose reinforcers are denoted with a W and an S, respectively. Standard errors are shown for each mean value.

duced significant main effects of duration, $F_{(2,10)} = 8.79$, $p < .05$, and upcoming reinforcer, $F_{(1,5)} = 14.87$, $p < .05$. In contrast to the duration effect observed with the shorter durations, local rates decreased as duration increased. For the 15, 45, and 90-s durations, mean local response rates were 51.31, 45.43, and 41.43, presses per minute, respectively. Mean local rates were again higher when the upcoming reinforcer was sucrose (54.27 presses per minute) than when it was wheel running (37.84 presses per minute).

Figure 12 shows wheel-running rates (revolutions per minute) in successive 5-s intervals for each reinforcer duration for each rat and the group. A paired *t*-test comparison of the wheel-running rates in the two 15-s conditions revealed that rates did not differ, $t_{(5)} = 1.43$, *ns*. In general, as duration increased, the running rate increased then decreased. For the 5, 10, 15, 15, 45, and 90-s durations, wheel-running rates were 36.80, 37.75, 40.05, 43.25, 32.86, and 27.81 revolutions per minute, respectively. A repeated measures ANOVA revealed a significant effect of duration, $F_{(5,25)} = 10.87$, $p < .05$. A similar relation occurred when rates during the initial 5-s interval were compared. This interval was common to every duration and represents the best point of comparison. Mean wheel-running rates during this initial interval were 36.80, 37.60, 39.81, 43.41, 31.34, and 23.49 revolutions per minute for the 5, 10, 15, 15, 45, and 90-s durations, respectively.

DISCUSSION

Varying the duration of an opportunity to run produced systematic changes in responding when wheel running was signaled. The effect did not occur until duration exceeded 15 s, beyond which overall rates declined. Changes in overall rates were a result of effects on both PRPs and local response rates. PRPs increased with wheel-running duration, but only in the presence of the wheel-running stimulus and only when durations were greater than 15 s. Local rates in the presence of a wheel-running stimulus showed a bitonic relation, increasing between 5 and 15 s, then decreasing beyond 15 s. Similarly, wheel-running rates increased as duration increased up to 15 s then decreased beyond 15 s.

Excitatory stimulus effects and inhibitory aftereffects both played roles in determining

lever pressing generated by the opportunity to run. PRPs lengthened and local rates decreased as duration increased between 15 and 90 s, but only in the presence of a stimulus signaling a wheel-running reinforcer. These changes appear to be the result of changes in the excitatory value of a stimulus signaling an opportunity to run. Type of prior reinforcer contributed to PRP duration; however, the effect was also limited to the presence of a stimulus signaling an opportunity to run and did not vary with duration.

The effect of wheel-running duration on lever pressing beyond 15 s is consistent with previous reports. Belke (1997) varied wheel-running reinforcer duration over values of 30, 60, and 120 s for rats responding on tandem FR 1 VI 30-s schedules of wheel-running reinforcement. As reinforcer duration increased, PRP duration increased, while local lever-pressing and wheel-running rates decreased. Belke and Dunbar (1998) varied reinforcer duration over values of 15, 30, and 90 s for rats responding on FI 60-s schedules. As reinforcer duration increased, PRPs increased while overall lever-pressing, local lever-pressing, and wheel-running rates decreased. Both investigations implied that PRP duration and local rates were linearly related to run duration. However, neither study investigated durations shorter than 15 s. The results of the present study show that although PRPs increase with duration as duration increased from 5 to 90 s, local and overall lever-pressing rates did not.

GENERAL DISCUSSION

The impetus for both the present study and that of Belke (2000) was the observation that the asymptotic rate of responding maintained by sucrose reinforcement was greater than that maintained by the opportunity to run within the same rat (Belke, 1998). This observation was inconsistent with the assumption of Herrnstein's (1970) hyperbolic form of the matching law that the asymptotic or maximal rate of responding should not vary with type of reinforcement. Belke's (2000) study concluded that the difference in asymptotic rates of responding generated by a drop of 15% sucrose solution and the opportunity to run for 15 s was largely a function of a

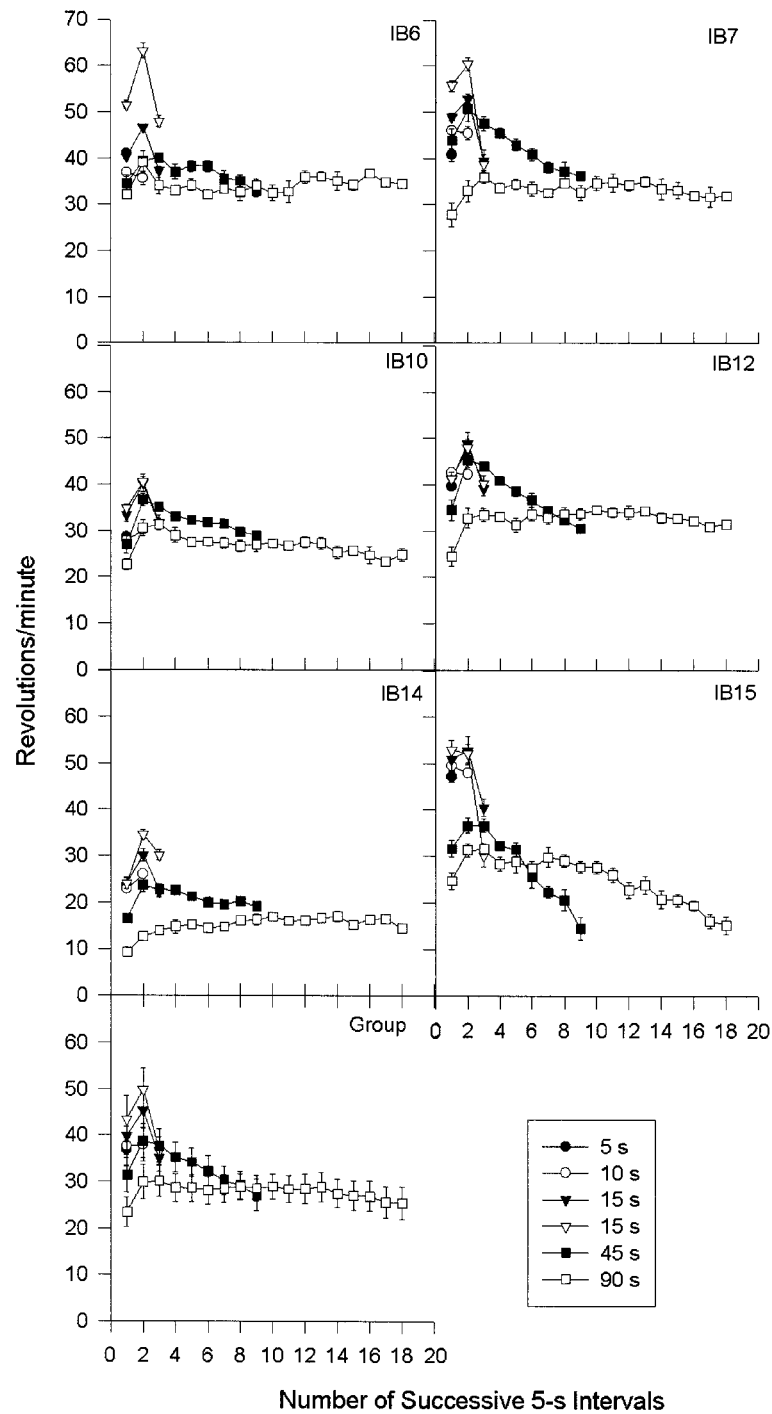


Fig. 12. Mean wheel-running rates (revolutions per minute) in successive 5-s segments of wheel-running reinforcers as a function of reinforcer duration for each rat and the group. Standard errors are shown for each mean.

difference in the excitatory value of the stimuli signaling the two reinforcers.

The results of the present study generally support this conclusion. The first experiment suggested that the opportunity to run for 15 s is a weak reinforcer that maintains responding at approximately the same level as a drop of 2.5% sucrose solution. Dallery, McDowell, and Lancaster (2000) showed that response rate asymptotes for lever pressing by rats maintained by sucrose solution were relatively constant across concentrations ranging from 21.9% to 6.8%, but decreased at concentrations of 3.4% and 1.7%. Concentration of 2.5% falls within the range of concentrations for which lower asymptotic response rates were observed by Dallery et al. The first experiment also showed that changes in operant responding that occurred when concentration was varied resulted from changes in the excitatory value of a stimulus signaling sucrose.

Both experiments provided evidence of an effect of prior reinforcers. In the first experiment, as the excitatory value of sucrose decreased, pauses following wheel running lengthened relative to those following sucrose. In the second experiment, when an opportunity to run was signaled, pauses were longer when the previous reinforcer was running. Common to both of these observations is that the excitatory value of the signaled reinforcer was low. Expression of an inhibitory aftereffect following a previous reinforcer within this paradigm appears to depend upon the excitatory value of the reinforcing event.

Also of interest was that the aftereffect in the second experiment did not vary with duration. If the aftereffect was momentary fatigue following a period of running, then one would expect that PRPs following a period of running would increase with the increase in revolutions run as reinforcer duration increased, but those following sucrose would not. Either the aftereffect is not momentary fatigue or the increase in duration between 15 and 90 s was not sufficient to produce a discernible change in muscular fatigue.

Momentary satiation is another candidate. Satiation for wheel running following a period of running would be expected to be stimulus specific. That is, following a period of running, satiation should affect responding in the presence of a stimulus signaling another opportunity to run, but not if the stimulus

signals a different reinforcer. This would account for longer pauses associated with wheel-running reinforcer to wheel-running reinforcer transitions, but not the pauses associated with sucrose reinforcer to wheel-running reinforcer transitions.

Two other possibilities related to recent research with wheel running are habituation (Aoyama & McSweeney, 2001) and a rewarding aftereffect (Lett, Grant, Byrne, & Koh, 2000). Aoyama and McSweeney demonstrated that wheel running showed effects of spontaneous recovery, dishabituation, and stimulus specificity which, the authors argue, are consistent with the suggestion that habituation plays a role in the regulation of wheel-running behavior. Although rats in their study ran freely in a wheel for a 30-minute period, demonstration of these effects suggests the possibility that habituation might be operating in the context of the opportunity to run over much briefer periods.

Lett et al. (2000) demonstrated that following the cessation of a period of running (i.e., 30 minute) rats experienced an aftereffect that conditioned a preference for a chamber associated with wheel running through backward conditioning. Although the duration of an opportunity to run used to produce this effect was considerably longer, it raises the possibility that the long pausing following running may be a function of this aftereffect. Future research can determine if habituation and this rewarding aftereffect occur with brief opportunities to run.

In summary, varying the concentration of sucrose reinforcers and the duration of wheel-running reinforcers resulted in changes in responding in the presence of the stimuli associated with these reinforcers that were largely due to changes in the excitatory value of the stimuli. Although both experiments provided evidence of inhibitory aftereffects, the role that they play appears to be limited.

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